AGGREGATED DISTRIBUTION OF *DIADEMA ANTILLARUM* IN A SHALLOW FOREREEF HABITAT

JAYA A. KAVEESHWAR, CHRIS D. CARSON
AND SHARON D. KARLSBERG

Abstract The 1983 mass mortality event of *Diadema antillarum* resulted in >99% decrease in urchin population and subsequent changes in abundance and composition of algal species. In recent years, urchin populations have begun to recover, yet distribution of *D. antillarum* is patchy within structurally complex habitat. This habitat provides effective refuge from predators and adverse wave conditions. *D. antillarum* may receive benefits from aggregation that outweigh the potential advantages of even distribution across suitable habitats. Transplant experiments confirm the suitability of unoccupied structurally complex areas. While transplanted urchins remained in structurally complex habitats, we did not observe changes in algal cover and species composition over the five day study period. It appears that low density populations of *D. antillarum* gain substantial benefits from aggregated distribution across suitable sheltering reef habitats.

INTRODUCTION (SDK)

The long-spined black urchin *Diadema antillarum* is a dominant algal grazer in the tropical coral reefs of the Caribbean Sea. In 1983, a water-borne pathogen caused a massive decrease in populations of *D. antillarum* throughout the Caribbean and western Atlantic. By 1984, the epidemic had reduced existing urchin numbers by 93-99% in all reef locations (Lessios 1988). In ten days during the summer of 1983, local mortality rates of *D. antillarum* on Jamaica's north shore reached almost 100% (Hughes et al. 1985). Postmortality recruitment patterns predicted that remnants of populations in each local area would start recruiting almost immediately. Such proportional recruitment would result in a monotonic density increase in *D. antillarum* populations (Lessios 1988). In Jamaica, however, only one of eleven locations showed a positive change in urchin population densities between 1983 and 1986; this increase was due to an accumulation of larger individuals, not an increase in urchin recruitment (Lessios 1988).

Pre-mortality estimates of *D. antillarum* on shallow forereefs ranged from 12.0-16.1 individuals/ m^2 (Hughes et al. 1985, Carpenter 1990, Copeland 1981). Post-mortality densities were almost 0 individuals/ m^2 (Swanson 1994). This rapid decline in *D. antillarum* populations strongly affected algal cover in reef habitats. In 1981, Carpenter examined feeding preferences in *D. antillarum* and found that urchins preferentially graze algal turfs at all reef sites (shallow and deep). While he observed some feeding on crustose forms of coralline algae, in all cases fleshy macroalgae was strongly avoided. Corresponding to these algal preferences, pre-dieoff algal cover consisted of 90% turf and 10% crustose forms. Only two months after the *D. antillarum* epidemic, turf constituted 50% of the algal cover and crustose forms accounted for only 1% of algal cover (Carpenter 1990). Without consistent grazing of *D. antillarum*, macroalgal species invaded reef substrates all over the Caribbean.

At present, *D. antillarum* populations are recovering, but urchin densities on the forereef remain low and are restricted to shallow depths (Swanson 1994). As algal biomass has remained high 12 years after the urchin dieoff (pers. obs.), food resources do not seem likely to determine distribution of urchins on the reef. Yet *D. antillarum* appears to be patchily distributed throughout the forereef, aggregating in groups in structurally complex substrates. We hypothesize that the availability of suitable refuge habitats has an important influence on the current distribution of *D. antillarum* at Discovery Bay, Jamaica.

Previous studies have shown that *D. antillarum* seeks structures which provide daytime refuge from predators and adverse wave conditions. Carpenter (1984) demonstrated that the frequency of homing behavior (fidelity to a particular rock crevice) is positively correlated with predator abundance. Likewise, urchins show a preference for dark areas, which are indicative of crevices, when experiencing adverse surge conditions (Morell 1981). Foster (1987) showed that urchin grazing was decreased during protracted periods of heavy wave action. This further indicates that *D. antillarum* seeks protective structure instead of grazing substrate when exposure conditions are unfavorable. Overall, structural complexity provides urchins with refuges from predation and adverse wave conditions. Thus availability of the these suitable structures is likely to influence distribution of *D. antillarum* populations on a coral reef.

We examined the distribution of *D. antillarum* on the west forereef of Discovery Bay Marine Laboratory, Jamaica. Population surveys and urchin transplant experiments were used to evaluate the following hypotheses.

1) *D. antillarum* is patchily distributed within reef habitats that have adequate structural complexity to provide suitable urchin refuges.

2) *D. antillarum* will remain in suitable refuge habitats when transplanted to unoccupied structurally complex sites in aggregated groups.

3) *D. antillarum* will not remain in flat habitats (with few suitable crevices for shelter) when transplanted in aggregated groups.

4) If urchins remain in a transplant habitat, they will reduce macroalgal cover in that area over time.

METHODS (NDC)

Survey. We surveyed substrate type and *D. antillarum* density in the 3-5 m depth range in the west forereef of Discovery Bay, Jamaica. We used three belt transects, 50 m, 45 m, and 50 m in length and 2 m in width, placed parallel to the reef crest starting from the canoe cut and ending south of the LTS mooring. The substrate was categorized according to three habitat classes: 1) structurally complex habitat: substrate with adequate crevices for *D. antillarum* to hide, 2) flat habitat: solid substrate with minimal *D. antillarum* shelter, and 3) sand and unconsolidated rubble. Within structurally complex habitat, the amount of area characterized by heavily grazed algal turf (currently or formerly occupied *D. antillarum* patch) was measured.

We looked at the degree of *D. antillarum* aggregation in the structurally complex habitat using an Index of Dispersion. Each area of suitable urchin habitat along the transect was divided into 1 m x 2 m quadrants. We calculated an Index of Dispersion value for these areas with the equation:

$$I = \sum (n_i - n)^2 / (m - 1)^* n$$

where n_i = number of *D. antillarum* in a given quadrant, n = average number of *D. antillarum* per quadrant, and m = number of quadrants. A value < 1 indicates even distribution, whereas a index value >1 indicates an clumped distribution.

To assess the density of *D. antillarum* within patches of heavily grazed algal turf, the patch area and number of *D. antillarum* per patch was assessed for five patches north of the canoe cut and five patches north of the LTS mooring. The patch area was an approximation of three-dimensional surface area with apparent intense *D. antillarum* grazing.

Experiment. Our study area was south of the LTS mooring in 3-5 m of water depth. We chose 15 sites of three different habitat types: 1) U sites: five sites with structurally complex substrate and *D. antillarum* populations of approximately 10 urchins; 2) N sites: five sites with no *D. antillarum* present, no evidence of *D. antillarum* grazing, and similar

structurally complex substrate; and 3) F sites: five sites with no *D. antillarum* present, no evidence of *D. antillarum* grazing, and flat substrate. A marker was placed in the center of each site, and the area of the N sites and F sites was defined as all area within a 2 m radius of the central marker.

We moved ten *D. antillarum* into each of the N sites on 3 March and ten *D. antillarum* into each of the F sites on 6 March. From 4-9 March we monitored the number of *D. antillarum* at the transplant sites (N and F) and pre-existing urchin patches (U sites) by careful examination of all crevices and overhangs in the site area.

In order to examine differences between the N and U sites, and assess possible evidence for *D. antillarum* grazing at the transplanted sites, we quantified substrate cover at each of the N and U sites. We used four line transects radiating out 1 m in the four cardinal directions from the central marking point. Along each transect, we measured percent cover of eight different cover categories: *Sargassum* sp., *Dictyota* sp. , *Padina* sp., *Turbinaria* sp., *Halimeda* sp., other macroalgae, live coral, and non-macroalgae cover. The N sites were assessed on 4-5 March, and again after four nights of potential grazing by the transplanted *D. antillarum*. U sites were assessed only once, and F sites were not assessed.

RESULTS (CDC)

Survey

Along the transects, we found that 64.8% of the area was structurally complex substrate with adequate urchin shelter, 24.3% was flat substrate with minimal urchin refuge, and 10.9% was a loose aggregation of sand and rubble. Of the habitat assessed as structurally complex, only 29.0% was algal turf.

We found 93 *D. antillarum* along the entire 290 m^2 belt transect; these were only present on the structurally complex substrate. The *D. antillarum* density over the entire transect area was 0.32 ind./m^2 , and the density in the structurally complex habitat was 0.49 ind./m^2. The *D. antillarum* were patchily within the structurally complex substrate, with an Index of Dispersion value of 5.36.

We found a positive correlation between patch size (surface area cleared) and number of urchins per patch (R^2 =0.64, $p<0.05$, Fig. 1). The variation in patch density within this small sample was large- from 0.94 ind/m^2 to 7.25 ind/m^2. with a mean density of 2.36 ind/m^2 (±SE of 0.60).

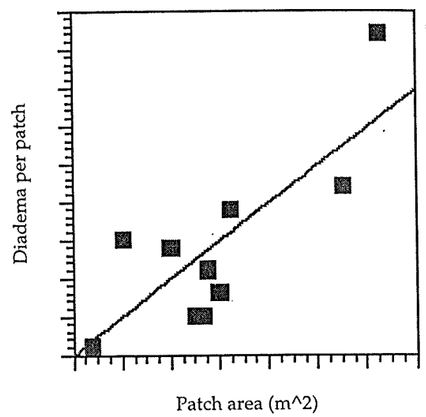

FIG. 1. *D. antillarum* number versus patch size for ten patches in the west forereef of Discovery Bay, Jamaica. Patch size was defined as the approximate surface area with heavily grazed algal turf. R^2=0.64, $p<0.05$

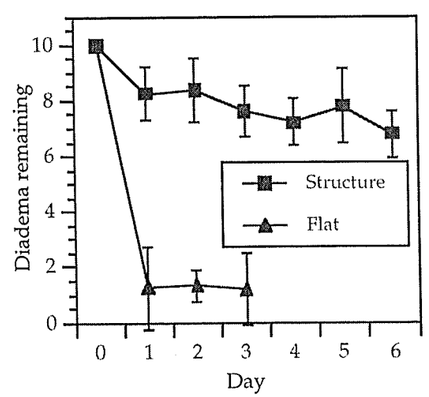

FIG. 2. Number of *D. antillarum* remaining at the transfer sites (mean ± SD, n=5) in structured areas with suitable urchin shelter (N sites), and flat sites with minimal urchin shelter (F sites).

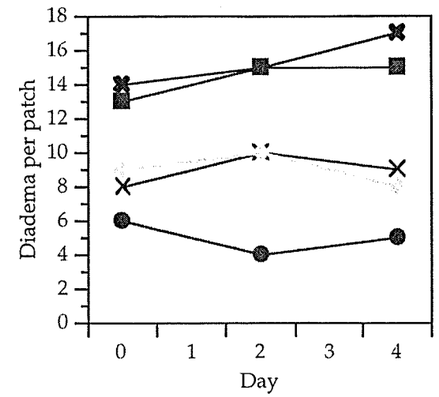

FIG. 3. Variation in *D. antillarum* number over four days of monitoring in the five marked sites in the west forereef of Discovery Bay.

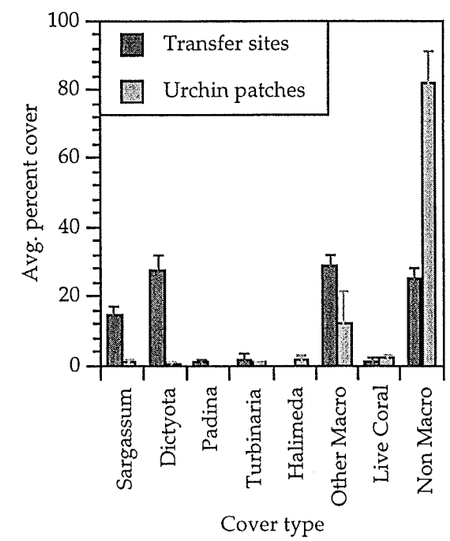

FIG. 4. Mean percent substrate cover (±SE) of transfer sites with rugged substrate and no previous urchin grazing (N sites, measured on March 4-5) and pre-existing urchin patches (U sites).

Experiment

The number of *D. antillarum* at the structurally complex N sites appeared to remain relatively constant for the period of six days (Fig. 2). The number of urchins at the flat F sites declined immediately after placement within the site area. The F sites containing suitable crevices or overhangs within the site area had one to three urchins remaining three days after transfer (Fig. 2). The difference between F sites and N sites in number of urchins remaining 3 days after placement was highly significant (students t-test, T=10.67, df=4, $p<0.001$).

The number of urchins at the five U sites remained fairly constant over the four days of monitoring (Fig. 3). The maximum change in urchin number over the four days was three urchins.

The difference in substrate cover in areas of intense grazing (U sites) and previously unoccupied areas (N sites) was obvious (Fig. 4). The N sites were dominated by tall macroalgae cover (>70%), whereas the U sites had only <15% macroalgae cover, consisting mostly of macroalgae turf < 2 cm tall (Fig. 4). There was no significant change in the substrate cover after four nights of potential grazing by the transplanted individuals. Differences found ranged from 0 to 3.5% change, well within the range of measuring error.

DISCUSSION (JAK)

D. antillarum was not found in flat, exposed areas, and consequently we tested whether urchins would be patchily distributed within structurally complex habitat. As predicted, the distribution of *D. antillarum* within the complex substrate habitat of the shallow forereef was clumped. The patchy distribution of *D. antillarum* in area we assessed as suitable refuge habitat may be the result of the following conditions:

1) The habitat is not suitable to *D. antillarum*.

2) *D. antillarum* is unable to disperse into unoccupied habitat.

3) *D. antillarum* chooses not to disperse into unoccupied habitat because it can benefit more from its current aggregated distribution Thus, aggregation outweighs the potential advantages of a more even distribution over suitable area.

Urchins transplanted into unoccupied areas with refuges remained in these sites which indicates the suitability of this structurally complex habitat. In contrast, urchins transplanted into flat, exposed areas rapidly vacated these sites. As both sites contain relatively equal assemblages of algae and differ only by the amount of structural complexity, the availability of shelter within a site appears to be an important determinant of habitat suitability. Therefore, a key question remains unanswered: Why are *D. antillarum* not evenly distributed across all suitable habitat since transplanted urchins remained in structurally complex sites?

D. antillarum may have dispersal limitations which prevent colonization of nearby habitat. This seems unlikely as the majority of the unoccupied structured habitat that we surveyed was adjacent to established urchin patches. *D. antillarum* migrates as much as 8 m during nocturnal foraging bouts (Carpenter 1984). Our results suggest that within established *D. antillarum* patches, populations are not rigidly fixed over time (Fig. 3). Although fluctuations in population size might be a result of sampling flaws (inability to detect all urchins within a site), varying population size might indicate urchin movement between patches. Therefore, *D. antillarum* should have access to neighboring unoccupied habitat.

It is more likely that *D. antillarum* receives tangible benefits from aggregation within a patch. As *D. antillarum* is a dioecious external spawner, gamete release by an isolated individual might result in low fertilization success (Levitan 1988). Therefore, a benefit of *D. antillarum* aggregation might be increased reproductive success from an aggregated and coordinated release of gametes.

Another benefit of aggregation may be increased access to desired food resources. *D. antillarum* strongly favors algal turf and crustose algae over mature macroalgae (Carpenter 1981). Our data supports this contention as sites with an established urchin assemblage had a substrate cover composed primarily of algal turf and crustose coralline algae (Fig. 4). *D. antillarum* avoids mature macroalgal forms because many have highly calcified tissue and high concentrations of toxic secondary metabolites (Hay 1994). Maintenance of algal turf requires a sufficiently high level of herbivory to prevent the growth of large macroalgae. If the herbivory rate of individual urchin is lower than the rate required to prevent macroalgal growth, the individual may not be able to maintain the desired turf and crustose algal growth. An aggregated group of *D. antillarum*, however, may have a collective rate of herbivory sufficiently high enough to maintain the turf and crustose algal growth. Therefore, *D. antillarum* may receive a nutritional benefit from living within an aggregated group.

Aggregation may also reduce *D. antillarum* susceptibility to dislodgment by strong current and may reduce predation risk. The formation of an interlocking matrix of spines by closely spaced *D. antillarum* neighbors may reduce current flow over the aggregated group, thus reducing the chance of individuals washing away during periods of heavy surge. Similarly, this "phalanx" formation may also make it more difficult for predators (such as triggerfish) to turn over individuals, exposing the less protected oral opening.

However, there may be costs to an aggregated existence. When population size reaches a threshold limit, food resources and refuge habitat may become limiting. Current *D. antillarum* population densities within aggregated patches are lower than overall pre-dieoff densities (2.36 ind./m^2 compared to 12-16 ind./m^2), indicating that food resources and refuges are not limiting.

Our final hypothesis tested the effects of transplanted urchin grazing on the algal communities of the previously unoccupied site. The limited duration of the experiment (six days) was probably not sufficient to get significant herbivory and corresponding changes in algal community.

Future studies should test if site fidelity of *D. antillarum* is density dependent. By placing different numbers of urchins in structurally complex habitat, we can examine whether urchin aggregation is necessary to maintain site fidelity. Furthermore, more time is necessary to assess grazing effects on algal cover. Long term studies could investigate the progression of macroalgal species decline due to preferential grazing by *D. antillarum*.

LITERATURE CITED

Carpenter, R. C. 1981. Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. Journal of Marine Research 39: 749-765.

Carpenter, R. C. 1984. Predation and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. Marine Biology 82: 101-108.

Carpenter, R. C. 1990. Mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. Marine Biology 104: 67-77.

Copeland, C. 1980. "The sea urchin is a most voracious an promiscuous feeding always ready to eat." Dartmouth Studies in Tropical Ecology, unpublished.

Foster, S. A. 1987. The relative impacts of grazing by Caribbean coral reef fishes and *Diadema*: effects of habitat and surge. Journal of Experimental Marine Biology and Ecology 105:1-20.

Hay, M. E., Q. E. Kappel, and W. Fenical. 1994. Synergisms in plant defenses against herbivores: interactions of chemistry, calcification, and plant quality. Ecology 75(b): 1714-1726.

Hughes, T. P., B. D. Keller, J. C. Jackson, and M. J. Boyle. 1985. Mass mortality of the echinoid *Diadema antillarum* (Philippi) in Jamaica. Bulletin of Marine Science 36(2): 377-384.

Lessios, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? Annual Review of Ecology and Systematics 19: 371-393.

Morell, L. 1981. Aggregational behavior of *Diadema antillarum*: a sticky business. Dartmouth Studies in Tropical Ecology, unpublished.

Swanson, A. N. and J. L. Bykowski. 1994. Potential limitations to *Diadema antillarum* distribution in a Jamaican forereef. pages 167-174 in J. L. Bykowski, editors Dartmouth Studies in Tropical Ecology. Hanover, New Hampshire, USA.